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Effects of ecological restoration on Orthoptera assemblages in a Mediterranean steppe rangeland

Jean-François Alignan · Jean-François Debras ·
Thierry Dutoit

Abstract In the last century, human activities have contributed to the fragmentation and the loss of 80 % of the original surface of a Mediterranean steppe rangeland in south-eastern France. In a recent ecological restoration project, an intensively cultivated orchard of 357 ha planted in 1987 among the steppe vegetation was rehabilitated as a herbaceous habitat for steppe birds after its abandonment in 2006. In addition, three experimental restoration treatments (nurse species seeding, hay transfer; soil transfer) were applied at large scale to test the restoration of the original steppe vegetation. Our four-year study aimed to assess the effect of this rehabilitation and the restoration treatments on Orthoptera assemblages. Capturing the Orthoptera with sweep nets, we measured species richness, abundance, Shannon index, Shannon evenness, Renkonen similarity index and two community structure indices. Our results reveal no significant differences in Orthoptera species richness, abundance and diversity between control and reference steppe after 4 years, indicating that the rehabilitation and the three restoration treatments did not significantly accelerate natural recolonization. In the last year of survey, Orthoptera abundances were still significantly lower in the restored treatments than in the original steppe. Thus, future monitoring will need to determine whether

abundance and structure similar to that of the reference steppe is achieved in these restored treatments.

Keywords Ecosystem rehabilitation · Grasshoppers · Grassland · Multi-taxonomic approach · Species-diversity

Introduction

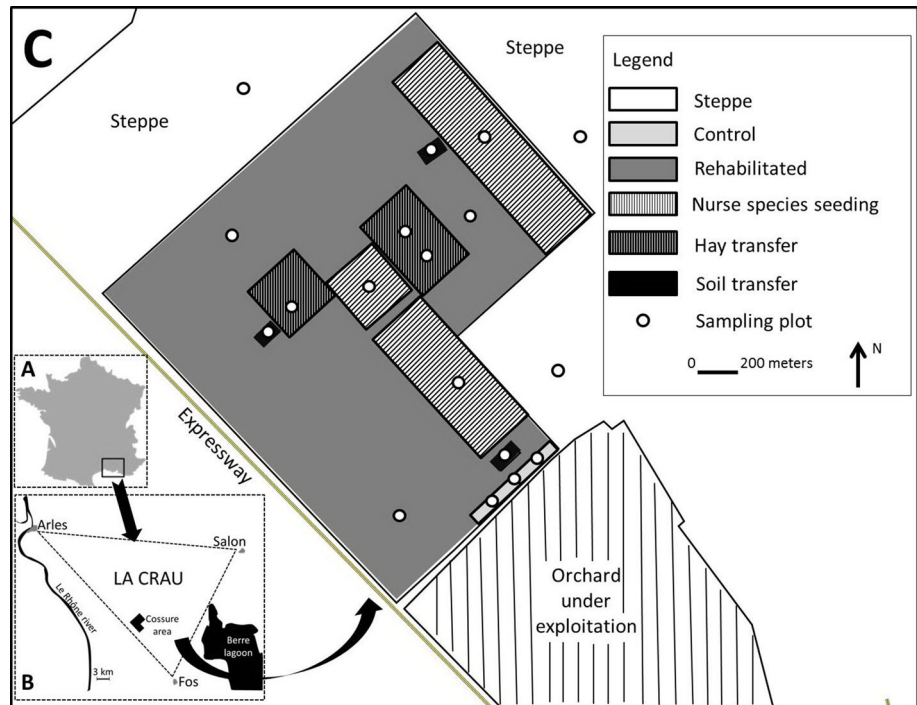
The impact of human activities leads to the fragmentation and loss of natural habitats (Saunders et al. 1991), which have been acknowledged as major threats for many species (Tscharntke et al. 2002). This is particularly true for ecosystems such as meadows, steppes or dry grasslands (Soons et al. 2005). These habitats are also known to be important for biodiversity. However, when thresholds of irreversible damage to these ecosystems are crossed, ecological restoration provides the opportunity to study the impact of restoration processes on degraded ecosystems in Europe (Aronson et al. 1993). Ecological restoration takes into account not only ecosystem functions but also overall biodiversity, insofar as its different compartments can be studied.

The Mediterranean region is characterized by its great diversity of ecosystems and landscapes, which have suffered destruction and degradation by anthropogenic activities. This led to a large number of ecological restoration projects, especially in aquatic environments: lakes (Beklioglu and Tan 2008; Papastergiadou et al. 2010; Prato et al. 2014), lagoons (Camacho et al. 2012; Rodrigo et al. 2013; Trabelsi et al. 2013) and rivers (Hughes et al. 2010; Trabucchi et al. 2012; Ontiveros et al. 2013). The numerous ecological restoration projects undertaken in terrestrial environments include forests (Pausas et al. 2004; Puértolas et al. 2010; Rey-Benayas et al. 2010; Schirone et al. 2011),

J.-F. Alignan (✉) · T. Dutoit
UMR CNRS/IRD 7263 IMBE, Institut Méditerranéen de
Biodiversité et Ecologie, Université d'Avignon et des Pays de
Vaucluse, IUT, Site Agroparc BP 1207,
84911 Avignon Cedex 9, France
e-mail: jean-francois.alignan@alumni.univ-avignon.fr

J.-F. Alignan · J.-F. Debras
INRA-UR 1115 Plantes et systèmes de cultures horticoles,
84000 Avignon, France

Fig. 1 **a** La Crau area located in southeastern France; **b** the abandoned Cossure orchard extends over the plain of La Crau; **c** the former Cossure orchard with the different treatments considered in this study: steppe (reference ecosystem); control; rehabilitated; nurse species seeding; hay transfer and soil transfer. The *black circles* refer to the sampling plots



wetlands (Mauchamp et al. 2002), grasslands (Traba et al. 2003), semiarid and arid ecosystems (Bonet 2004; Maestre and Cortina 2004; Le Houérou 2000; Josa et al. 2012), and steppes (Maestre et al. 2006).

The present study is part of the biggest terrestrial ecological restoration project in France, covering 357 ha of a Mediterranean steppe rangeland (near 43°30'N and 4°51'E) previously degraded because of its transformation into an intensively cultivated orchard between 1987 and 2006. It was bordered to the south by an expressway linking Marseille city and Arles city, to the east by another peach orchard still under exploitation and to the north and the northwest by the original steppe vegetation (Fig. 1).

The planting of the Cossure orchard was carried out between 1987 and 1992. In 2006, it was totally abandoned after a bankruptcy. In 2008, biological studies of the abandoned orchard began as part of a survey of the initial state before its planned rehabilitation close to its earlier steppe rangeland ecosystem, which still exists in the area around the orchard. Several compartments of biodiversity were initially considered: vegetation, avifauna and insects (beetles and Orthoptera) (for details, see Dutoit et al. 2013a).

The study on steppe birds highlighted the need for an ecological rehabilitation project to facilitate their return. Thus, in 2009, rehabilitation was undertaken, consisting of the removal of 200,000 peach trees, of 100,000 poplars constituting the hedgerows and of 55 km of irrigation pipes. The rehabilitation period ended with the leveling of the soil surface and the return of sheep grazing to the

former orchard in March 2010 (Dutoit et al. 2013a). Steppe birds were rapidly observed on the abandoned orchard after its rehabilitation into a species-poor spontaneous herbaceous plant community (Wolff 2010). Nevertheless, colonization by the characteristic steppe plant species has been much slower (Jaunatre et al. 2012, 2014).

Thus, to enhance restoration of the typical steppe vegetation, a range of ecological restoration treatments (nurse species seeding; hay transfer; soil transfer) were undertaken between March and November 2009 on a large scale over the ecological rehabilitation area (Jaunatre et al. 2012; Dutoit et al. 2013b). Three nurse species (*Lolium perenne*, *Festuca arundinacea* and *Onobrychis sativa*) were sown on 60 ha in order to promote the establishment of a typical steppe vegetation structure and to prevent weed species from occupying the new free trophic niches. The hay, collected by air-vacuuming, was transferred over 20 ha in order to afford the seed bank of the typical vegetation of the steppe. The soil transferred, which was going to be destroyed by a quarry extension, was a 20 cm upper soil layer spread over 3 ha in order to afford a pool of propagules of typical steppe vegetation and their associated microorganisms (Jaunatre et al. 2012, 2014). These experiments have the advantage of enhancing the ecosystem's passive restoration by active restoration through human intervention, which is the principle behind restoration ecology (Dobson et al. 1997).

Here, Orthoptera assemblages were the target of our experimental ecological restoration study. Orthoptera are

known to be major components of grassland ecosystems (Odum et al. 1962; Gandar 1982; Joern 1982a; Samways and Lockwood 1998; Kati et al. 2003). They play a central role, being major primary consumers of grassland vegetation (Joern 1982a, 1986; O'Neill et al. 2003) and they constitute an important source of prey for predators such as birds, spiders and lizards (Joern 1986; Belovsky and Slade 1993; Parr et al. 1997; Oedekoven and Joern 1998). Joern (1982b) summarized the various factors that drive their choice of habitat: vegetation structure and species number, microclimate (temperature, humidity and light intensity), soil characteristics, food plant availability and suitable sites for oviposition. For these reasons, Orthoptera are considered as good bioindicators to characterize habitats and environmental changes or naturalness (Báldi and Kisbenedek 1997; Bazelet and Samways 2011). In the plain of La Crau, Orthoptera are a very important community (Léonide 1983). They constitute one of the main average annual Arthropod biomasses (Bigot et al. 1983) and are a major source of prey for birds (Foucart 1997).

The aim of this study was to assess the effects of ecological rehabilitation and experimental vegetation restoration on Orthoptera assemblages. To measure these effects, species richness, abundance, composition and structure of the Orthoptera assemblages were considered. The study was undertaken over 4 years (2010–2013). To explain the possible variations measured, local habitat variables were also measured. We hypothesized that: (1) the response of Orthoptera assemblages would show variations throughout the 4 years of the survey (2010–2013); (2) the presence of Orthoptera assemblages close to those of the steppe reference ecosystem in the first years after rehabilitation and application of the different restoration treatments would be a good indication of the short-term success of ecological restoration, allowing us to confirm changes in plant community structure (density, height, plant cover) and the emergence of a favorable habitat for the steppe characteristic entomofauna used as the reference ecosystem in this restoration project.

Materials and methods

Study area: the plain of La Crau in south-eastern France

Located ~50 km north-west of Marseille in south-eastern France and at the center of the triangle formed by the cities of Arles, Salon de Provence and Fos-sur-Mer, the plain of La Crau extends over 11,500 ha in several fragmented areas (Fig. 1). Since the 16th century, human activities (cultivation, industries) have contributed to the loss of 80 % of its original surface (Buisson and Dutoit 2006). Formerly the delta of the Durance River, this plain is

considered by plant ecologists as a steppe (Devaux et al. 1983) characterized by three factors that shape the landscape: climate, topography and traditional sheep grazing. The climate is dry with average temperatures of 14.5 °C, yearly precipitation of 500–600 mm and winds of more than 50 km h⁻¹ over 110 days a year (Devaux et al. 1983). The steppe is characterized by an extremely flat topography, a soil surface 50 % covered by siliceous stones and a soil depth of 40 cm covering an impermeable calcareous conglomerate which does not allow plant roots access to groundwater (Colomb and Roux 1978). Finally, for several millennia there has been itinerant sheep grazing on the steppe (Badan et al. 1995; Henry et al. 2010), turning the plain of La Crau into the open landscape of a typical Mediterranean rangeland.

Experimental design

The study on Orthoptera was a four-year monitoring survey (2010–2013) on different areas: steppe area, the reference ecosystem; control area (only removal of trees); rehabilitated area (tree removal, soil leveling, re-introduction of sheep grazing) and restoration treatment areas (rehabilitated + nurse species seeding or hay transfer or soil transfer). For each area, three sampling plots were considered and each of these plots was subdivided into seven transects. The transects, 40 m long and 2 m wide, were arranged 10 m apart (Evans 1984) to avoid proximity effects (Picaud and Petit 2007).

Orthoptera sampling

Orthoptera were captured using a sweep net, which is the sampling method most commonly used to obtain fairly accurate estimations of the relative abundance and species composition of Orthoptera in short herbaceous vegetation (Evans 1984; Gardiner et al. 2005). The net was 38 cm diameter (Bomar 2001; O'Neill et al. 2003; Gardiner et al. 2005; Batáry et al. 2007). We followed the standard procedure for sampling Orthoptera in vegetation: once back and forth in a 180° arc in front of the sampler along a straight line at a steady speed (Evans 1984; Kemp et al. 1990; Báldi and Kisbenedek 1997; O'Neill et al. 2003; Gardiner et al. 2005). Along the 40 m transect, the number of sweeps was >50, which is relatively high for estimating Orthoptera density (Fuhlendorf et al. 2002; Gardiner et al. 2005). Samples were collected during the peak activity of the species, namely when sunshine is at a maximum (Guido and Gianelle 2001). In La Crau, Foucart (1997) reported that imago densities greatly increase in July, which is why the sampling was undertaken during that month. The contents of the sweep net were emptied into plastic bags (Evans 1984) and subsequently brought to the laboratory.

Then, the Orthoptera were anesthetized using CO₂, a gas inducing temporary sleep (Gilmour and Robinson 1964; Mead et al. 1988; Dupuy 2009). We identified the individuals on the basis of *Faune de France* (Chopard 1951), and the identification key of Bellmann and Luquet (1995). The next day, Orthoptera were returned to the exact place where they had been collected.

Habitat variables

During Orthoptera sampling, habitat variables were collected. For each of the seven transects at each sampling plot in each area, three quadrats of 2 m by 2 m were used to estimate the percentage of bare ground, stones and vegetation cover. Average vegetation height, an important factor for Orthoptera populations (Tatin et al. 2000), was measured using a graduated measuring device.

Data analysis

For the statistical analysis, to ensure representativeness of the Orthoptera assemblage sampling, all data obtained at each sampling plot of the different areas were pooled. Because a single transect is not representative enough of the Orthoptera assemblages, we pooled the seven transects in each sampling plot (Evans 1984).

In order to assess the effects of ecological rehabilitation and restoration on Orthoptera assemblage characteristics, species richness, abundance, Shannon index, Shannon evenness and Renkonen similarity index were considered, using the normalized Community Structure Integrity Index (CSII_{norm}) and the Higher Abundance Index (HAI). The CSII_{norm} is a synthetic indicator developed to assess community or assemblage resilience and restoration success (Jaunatre et al. 2013). Based on abundances, it measures the proportion of the species of the steppe assemblages that is present in the assessed areas (rehabilitated, restored and control in our study). It is bounded between 0 and 1: 0 means that no species of the reference ecosystem are present in the assessed area and 1 means that the proportion of the species abundance in the assessed area is exactly the same as the proportion of the species abundance in the reference ecosystem (Jaunatre et al. 2013). The HAI quantifies the proportion of the species abundance in the assessed assemblages exceeding that in the steppe assemblages (Jaunatre et al. 2013). This index is bounded between 0 and 1. The index increases when non-target species abundance increases or when target species abundance increases to above their abundance in the reference ecosystem (Jaunatre et al. 2013).

Taking the 4 years of the survey in these six areas, we first considered the interaction between years and areas. Parametric conditions were not reached, so we did not test

this interaction. Nevertheless, species richness, abundance, Shannon index, Shannon evenness, Renkonen similarity index, CSII_{norm}, HAI almost always reached parametric conditions either for the year effect or for the area effect. Thus, means were compared: (1) within one area among the 4 years and (2) among the six areas for the last year of survey, either using one-way ANOVA followed by Tukey's test allowing pairwise comparison when parametric conditions were met, or using the Kruskal–Wallis test followed by the Wilcoxon–Mann–Whitney test. Box–Cox–transformation was applied on the ANOVA performed. Orthoptera composition was ordinated by Non-Metric Multidimensional Scaling (NMDS) based on Orthoptera abundance. Habitat characteristics were ordinated by a Principal Component Analysis (PCA). All analyses were conducted with R 2.15.3 (R-Development-Core-Team 2011) with the additional packages *ade4* (Chessel et al. 2004; Dray and Dufour 2007), *mass* (Venables and Ripley 2002) and *vegan* (Oksanen et al. 2008).

Results

Effects of rehabilitation and restoration on Orthoptera assemblage characteristics

In the control and steppe areas, species richness declined significantly from the first year to the second year and recovered in the third and fourth years (Fig. 2a). In the rehabilitated, nurse species seeding, hay transfer and soil transfer areas, there were no significant differences among the 4 years of the survey (Fig. 2a). In the last survey year, there were no significant differences in species richness between the steppe (11.67 ± 0.51) and the other areas: control (7.67 ± 0.51), rehabilitated (11.67 ± 1.39), nurse species seeding (8 ± 1.15), hay transfer (6.67 ± 0.51) and soil transfer (9 ± 0.56 ; Table 1).

Regarding Orthoptera abundance, there was a significant increase between the second and the third year in the control area and between the third and the fourth year in the rehabilitated area (Fig. 2b). However, the three restoration treatments (nurse species seeding, hay transfer and soil transfer) and the steppe showed no significant differences among the 4 years of the survey (Fig. 2b). In the last year, significant differences were measured between the steppe and the three restoration treatments (Table 1). The highest abundance in the last survey year was found in the steppe (81 ± 3.84), but did not differ significantly from the control (63.67 ± 5.85) and the rehabilitated area (72.67 ± 6.17 ; Table 1).

In the control area, the Shannon index decreased continuously during the 4 years of the survey (Table 2). In the rehabilitated and nurse species seeding areas, the Shannon

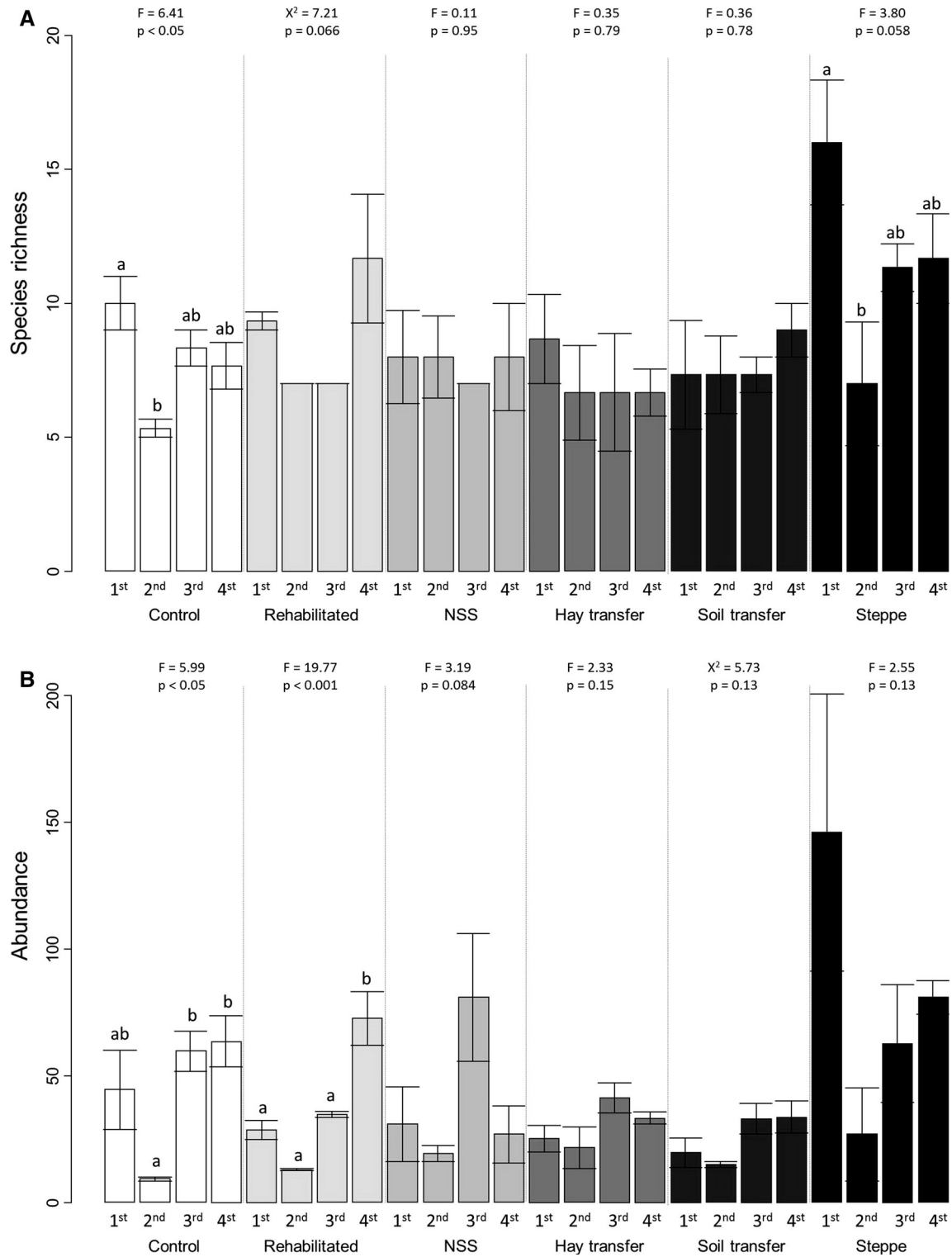


Fig. 2 Means and standard errors of species richness (a) and abundance (b) during the four-year survey (2010–2013) for each area: control (white), rehabilitated (light gray), nurse species seeding (NSS) (gray), hay transfer (dark gray), soil transfer (very dark gray) and steppe (black). F and p values of ANOVAs or χ^2 and p values of

Kruskal–Wallis tests performed to compare the 4 years within each area are given above each area. Bars sharing a common letter have no significant differences according to Tukey post hoc test or Wilcoxon–Mann–Whitney test

Table 1 Orthoptera assemblage characteristics for each area in 2013 (last year of survey): control, rehabilitated, nurse species seeding (NSS), hay transfer, soil transfer and steppe

| | ANOVA | Control | Rehabilitated | NSS | Hay transfer | Soil transfer | Steppe |
|------------------|------------------------------------|-----------------|-----------------|----------------|-----------------|-----------------|-----------------|
| Species richness | df = 5 F = 1.77 <i>p</i> = 0.19 | 7.67 ± 0.51 ns | 11.67 ± 1.39 ns | 8 ± 1.15 ns | 6.67 ± 0.51 ns | 9 ± 0.56 ns | 11.67 ± 0.96 ns |
| Abundance | df = 5 F = 7.42 <i>p</i> < 0.01 | 63.67 ± 5.85 ab | 72.67 ± 6.17 ac | 27 ± 6.49 b | 33.33 ± 1.35 bc | 33.67 ± 3.67 bc | 81 ± 3.84 a |
| Shannon index | df = 5 F = 0.84 <i>p</i> = 0.54 | 2.11 ± 0.12 ns | 2.64 ± 0.15 ns | 2.62 ± 0.15 ns | 2.24 ± 0.18 ns | 2.59 ± 0.07 ns | 2.58 ± 0.17 ns |
| Evenness | df = 5 F = 1.56 <i>p</i> = 0.24 | 0.72 ± 0.02 ns | 0.77 ± 0.05 ns | 0.90 ± 0.01 ns | 0.82 ± 0.03 ns | 0.82 ± 0.02 ns | 0.73 ± 0.05 ns |
| Renkonen index | df = 4 F = 0.72 <i>p</i> = 0.59 | 0.44 ± 0.02 ns | 0.36 ± 0.02 ns | 0.42 ± 0.02 ns | 0.39 ± 0.01 ns | 0.47 ± 0.02 ns | |
| CSII norm | df = 5 F = 4.49 <i>p</i> < 0.05 | 0.64 ± 0.01 ab | 0.59 ± 0.07 ab | 0.34 ± 0.07 b | 0.39 ± 0.04 b | 0.50 ± 0.05 ab | 1.00 ± 0.09 a |
| HAI | df = 5 F = 1.44 <i>p</i> = 0.28 | 0.42 ± 0.06 ns | 0.54 ± 0.08 ns | 0.26 ± 0.07 ns | 0.36 ± 0.05 ns | 0.19 ± 0.02 ns | 0.33 ± 0.04 ns |

For each characteristic, the given values are mean ± standard errors, df (degree of freedom), F and *p* values resulting from the ANOVAs performed to test the effect of each area on each characteristic. Two boxes with a common letter have significantly different values according to Tukey post hoc test (*ns* when non-significant)

index decreased significantly between the first and the third year and then recovered between the third and the fourth year (Table 2). In the hay transfer and soil transfer areas, no significant differences were measured for the Shannon index during the 4 years (Table 2). In the steppe, the Shannon index decreased significantly between the first and the second year and then remained steady during the next two years (Table 2). In the nurse species seeding, hay transfer and rehabilitated areas, Shannon evenness significantly decreased between the first and the third year and then recovered in the fourth year (Table 2). In the control, soil transfer and steppe areas, Shannon evenness did not significantly differ over the course of the 4 years (Table 2).

In the last year of the survey, neither Shannon index nor Shannon evenness showed any significant differences among the six areas considered (Table 1).

Between the steppe and the control, rehabilitated, hay transfer and soil transfer areas, the Renkonen similarity index decreased significantly between the first and the second year and then increased during the next 2 years (Table 2). In the last year of the survey (2010), there were no significant differences between the steppe and the other areas (Table 1).

The NMDS ordination, based on abundance, highlighted the high variability in the composition of Orthoptera assemblages in all the areas considered (Fig. 3a). No species were typical of one specific area, as all the areas were close to each other in the ordination. Figure 3b shows the successions of Orthoptera assemblages for each area from year to year. The trajectories of the barycenter of the control, restored and rehabilitated areas were shown to be very dynamic from the first to the fourth year of the survey.

The trajectory of the barycenter of the steppe area was also shown to be dynamic, although less so than the other areas.

In the control and rehabilitated areas, the CSII norm increased significantly between the first and the fourth year of the survey (Table 2). In the nurse species seeding, hay transfer and soil transfer areas, the CSII norm showed no significant differences among the 4 years of the survey (Table 2). In 2013, the CSII norm differed significantly between the steppe (1.00 ± 0.09) and nurse species seeding (0.34 ± 0.07) and hay transfer (0.39 ± 0.04; Table 1). No significant difference in the CSII norm was measured between the steppe and the control (0.64 ± 0.01), the rehabilitated (0.59 ± 0.07) and soil transfer (0.50 ± 0.05) areas (Table 1).

In the steppe, the HAI remained stable throughout the 4 years (Table 2). All the other areas showed an increase between the first and the second year (Table 2). Then, between the second and the fourth year, the control and rehabilitated areas remained stable while the three restoration treatments showed a significant decrease (Table 2). In 2013, no significant difference was observed between the steppe (0.33 ± 0.04) and all the other areas [lowest value in soil transfer (0.19 ± 0.02) and highest value in rehabilitated (0.54 ± 0.08; Table 1)].

Habitat characteristics

The PCA ordination based on habitat characteristics in 2013 showed bare soil cover and stone cover to be in opposition to vegetation height and vegetation cover on the first axis (76.6 %; Fig. 4). The steppe area was correlated with bare soil and stone cover while rehabilitation and

Table 2 Orthoptera assemblage characteristics for the 4 years survey for each area: control, rehabilitated, nurse species seeding (NSS), hay transfer, soil transfer and steppe

| | Control | | | | Rehabilitated | | | | |
|----------------|--------------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| | 1st | 2nd | 3rd | 4th | 1st | 2nd | 3rd | 4th | |
| Shannon index | df = 3 F = 5.49 p < 0.05 | 3.02 ± 0.05 a | 2.25 ± 0.07 b | 2.50 ± 0.15 ab | 2.11 ± 0.12 b | 3.00 ± 0.02 a | 2.63 ± 0.02 ab | 1.94 ± 0.12 b | 2.64 ± 0.15 ab |
| Evenness | df = 3 F = 3.65 p = 0.06 | 0.91 ± 0.01 ns | 0.93 ± 0.01 | 0.82 ± 0.06 | 0.72 ± 0.02 | 0.93 ± 0.01 a | 0.94 ± 0.01 a | 0.69 ± 0.04 b | 0.77 ± 0.05 ab |
| Renkonen index | df = 3 F = 4.89 p < 0.01 | 0.53 ± 0.01 | 0.26 ± 0.02 b | 0.42 ± 0.02 ab | 0.44 ± 0.02 ab | 0.38 ± 0.01 | 0.20 ± 0.01 b | 0.42 ± 0.02 | 0.36 ± 0.02 ab |
| CSIInorm | df = 3 F = 10.9 p < 0.01 | 0.35 ± 0.07 a | 0.29 ± 0.04 a | 0.54 ± 0.01 ab | 0.64 ± 0.01 b | 0.24 ± 0.03 a | 0.36 ± 0.03 ab | 0.51 ± 0.01 b | 0.59 ± 0.07 b |
| HAI | df = 3 F = 5.95 p < 0.05 | 0.19 ± 0.02 a | 0.57 ± 0.06 b | 0.61 ± 0.03 b | 0.42 ± 0.06 ab | 0.19 ± 0.04 a | 0.61 ± 0.04 b | 0.39 ± 0.01 ab | 0.54 ± 0.08 ab |
| NSS | | | | | | | | | |
| Shannon index | df = 3 F = 6.10 p < 0.05 | 2.54 ± 0.13 a | 2.56 ± 0.21 a | 1.23 ± 0.15 b | 2.62 ± 0.15 a | 2.80 ± 0.13 ns | 2.17 ± 0.15 ns | 1.84 ± 0.23 ns | 2.24 ± 0.18 ns |
| Evenness | df = 3 F = 12.8 p < 0.01 | 0.88 ± 0.03 a | 0.86 ± 0.03 a | 0.44 ± 0.05 b | 0.90 ± 0.01 a | 0.92 ± 0.01 a | 0.83 ± 0.02 ab | 0.70 ± 0.03 b | 0.82 ± 0.03 ab |
| Renkonen index | df = 3 F = 1.22 p = 0.32 | 0.42 ± 0.02 ns | 0.30 ± 0.02 ns | 0.39 ± 0.01 ns | 0.42 ± 0.02 ns | 0.44 ± 0.01 a | 0.17 ± 0.02 b | 0.39 ± 0.02 a | 0.39 ± 0.01 a |
| CSIInorm | df = 3 F = 2.55 p = 0.13 | 0.26 ± 0.07 ns | 0.62 ± 0.07 ns | 0.56 ± 0.03 ns | 0.34 ± 0.07 ns | 0.25 ± 0.03 ns | 0.40 ± 0.09 ns | 0.48 ± 0.03 ns | 0.39 ± 0.04 ns |
| HAI | df = 3 F = 7.93 p < 0.01 | 0.17 ± 0.06 a | 0.55 ± 0.01 ab | 0.68 ± 0.04 b | 0.26 ± 0.07 a | 0.01 ± 0.01 a | 0.73 ± 0.02 c | 0.50 ± 0.04 bc | 0.36 ± 0.05 b |
| Soil transfer | | | | | | | | | |
| Shannon index | df = 3 F = 0.51 p = 0.68 | 2.38 ± 0.21 ns | 2.44 ± 0.27 ns | 2.05 ± 0.10 ns | 2.59 ± 0.07 ns | 3.45 ± 0.05 a | 2.20 ± 0.18 b | 2.72 ± 0.07 b | 2.58 ± 0.17 b |
| Evenness | df = 3 F = 0.72 p = 0.57 | 0.86 ± 0.01 ns | 0.85 ± 0.05 ns | 0.73 ± 0.06 ns | 0.82 ± 0.02 ns | 0.87 ± 0.02 ns | 0.87 ± 0.04 ns | 0.78 ± 0.03 ns | 0.73 ± 0.05 ns |

Table 2 continued

| | Control | | | | Rehabilitated | | | |
|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| | 1st | 2nd | 3rd | 4th | 1st | 2nd | 3rd | 4th |
| Renkonen index | 0.36 ± 0.01 ab | 0.24 ± 0.02 a | 0.39 ± 0.02 ab | 0.47 ± 0.02 b | | | | |
| | df = 3 | | | | | | | |
| | F = 5.02 | | | | | | | |
| | p < 0.01 | | | | | | | |
| CSII norm | 0.19 ± 0.03 ns | 0.43 ± 0.07 ns | 0.44 ± 0.04 ns | 0.50 ± 0.05 ns | 1.00 ± 0.14 ns | 1.00 ± 0.29 ns | 1.00 ± 0.12 ns | 1.00 ± 0.09 ns |
| | df = 3 | | | | | | | |
| | F = 3.01 | | | | | | | |
| | p = 0.09 | | | | | | | |
| HAI | 0.04 ± 0.01 a | 0.59 ± 0.07 b | 0.45 ± 0.01 bc | 0.19 ± 0.02 ac | 0.22 ± 0.07 ns | 0.28 ± 0.08 ns | 0.25 ± 0.07 ns | 0.33 ± 0.04 ns |
| | df = 3 | | | | | | | |
| | F = 16.6 | | | | | | | |
| | p < 0.001 | | | | | | | |

For each characteristic, the given values are mean ± standard errors, df (degree of freedom), F and p values resulting from the ANOVAs performed to test the effect of each area on each characteristic. Two boxes with a common letter have significantly different values according to Tukey post hoc test (ns when non-significant)

Fig. 3 NMDS ordination based on 72 samples and the 23 species present in at least three samples. The **a** plot shows only the 2013 samples by area: control (white), rehabilitated (light gray), nurse species seeding (NSS) (gray), hay transfer (dark gray), soil transfer (very dark gray) and steppe (black). The **b** plot shows the succession of Orthoptera assemblages for each area, according to the position of their barycenter: solid arrows represent the succession from the first year (1st = 2010) to the second year (2nd = 2011); dashed arrows represent the succession from the second year (2nd = 2011) to the third year (3rd = 2012); bold arrows represent the succession from the third year (3rd = 2012) to the fourth year (4th = 2013)

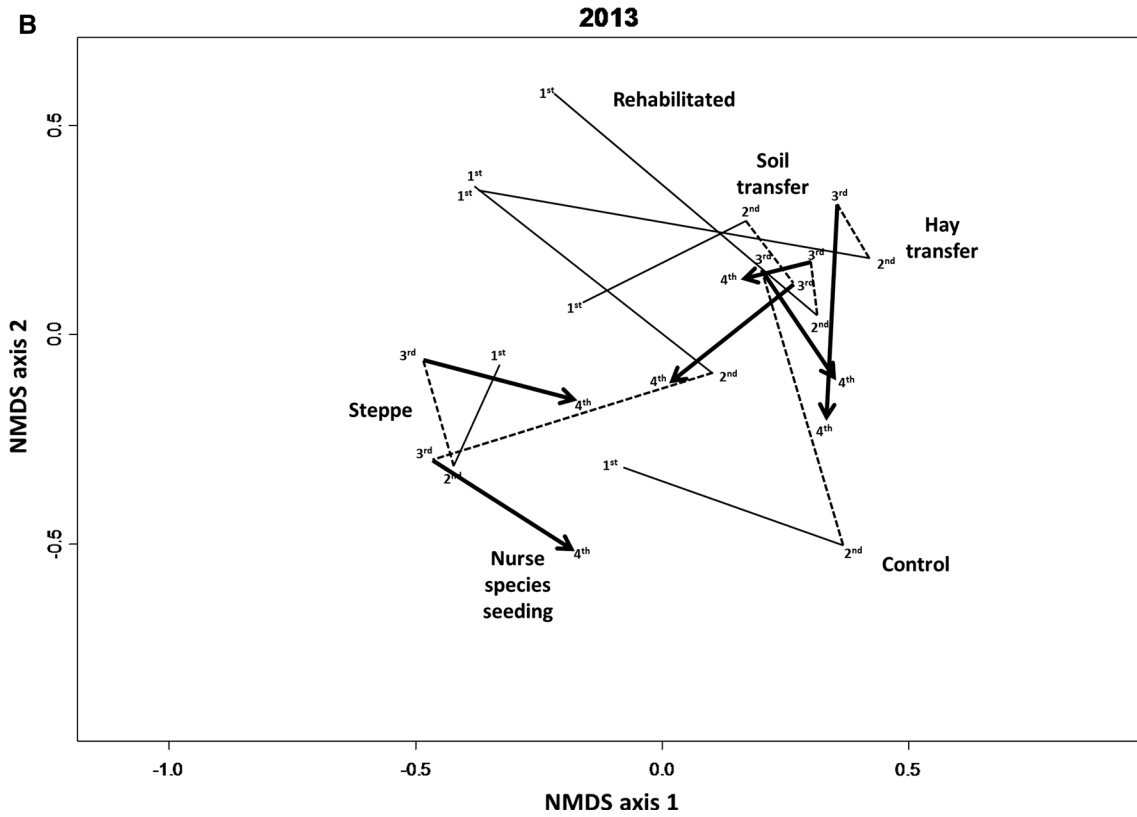
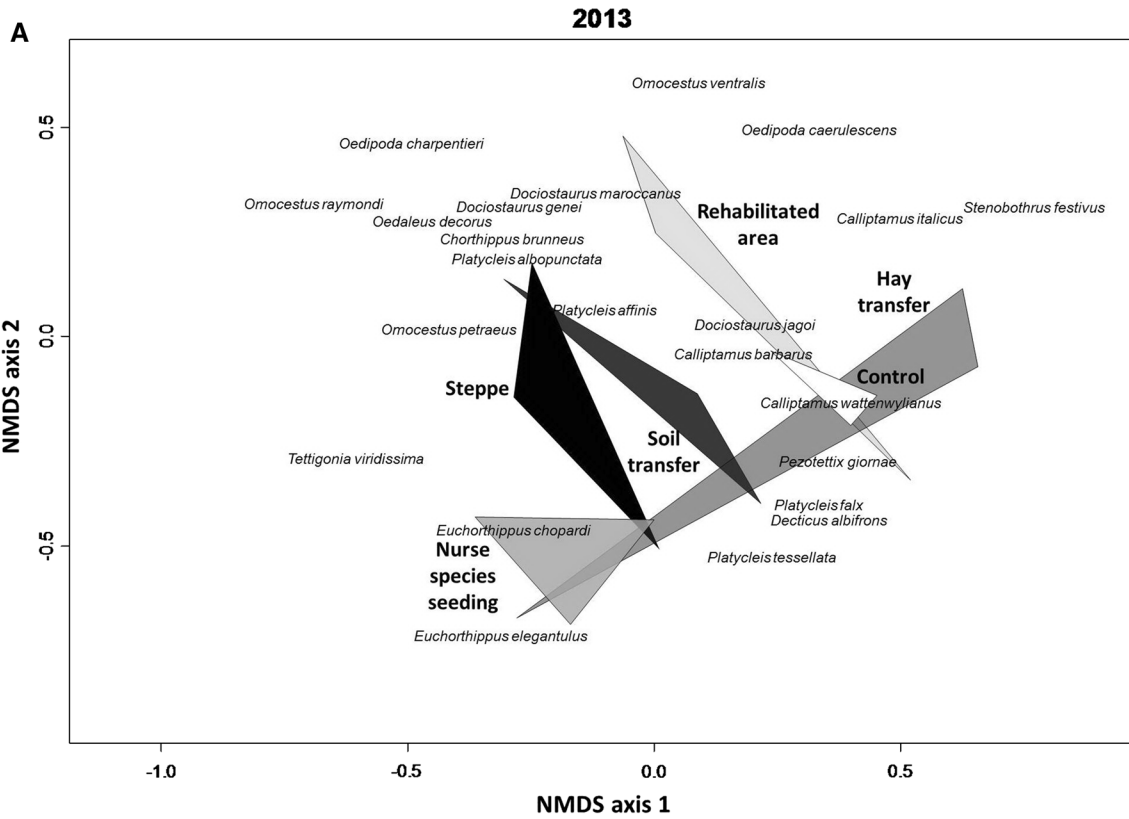
restoration treatments were correlated with vegetation cover. Vegetation height was correlated with nurse species seeding and control areas.

Discussion

Effects of restoration and rehabilitation on Orthoptera assemblages

In this study, the Orthoptera assemblages assessed over 4 years included twenty-three species (17 *Acrididae* and 6 *Tettigoniidae*). 3,100 individuals were captured and then released in the different areas considered (control; rehabilitated area; nurse species seeding; hay transfer; soil transfer; steppe, i.e. the reference ecosystem). All these species were common in the La Crau area. The two Orthoptera red-listed species of La Crau (*Prionotropis hystrix rhodanica* and *Saga pedo*) were absent in our study site. When we assessed the effects of restoration and rehabilitation on Orthoptera assemblages, it became clear that neither habitat rehabilitation nor the additional active restoration of vegetation (nurse species seeding; hay transfer; soil transfer) favored Orthoptera by accelerating their natural recolonization. Generally, typical Orthoptera species of the steppe of La Crau were present throughout the Cossure area, the composition of typical Orthoptera assemblages being found already 4 years after the abandonment of the orchard. The structure of these typical Orthoptera assemblages was almost identical in every area considered here. Surprisingly, however, abundances were still significantly lower for all three restoration treatments compared with the reference steppe ecosystem!

Four years after the rehabilitation and the restoration, species richness and diversity did not significantly differ between the steppe and all the other areas. With respect to species richness, it has already been proved in other ecosystems that Orthoptera were a taxonomic group whose response to ecological restoration was rapid and positive (Gebeyehu and Samways 2002; Nemeč and Bragg 2008; Borchard et al. 2013). Regarding abundance, we showed here that 4 years after rehabilitation and restoration, there



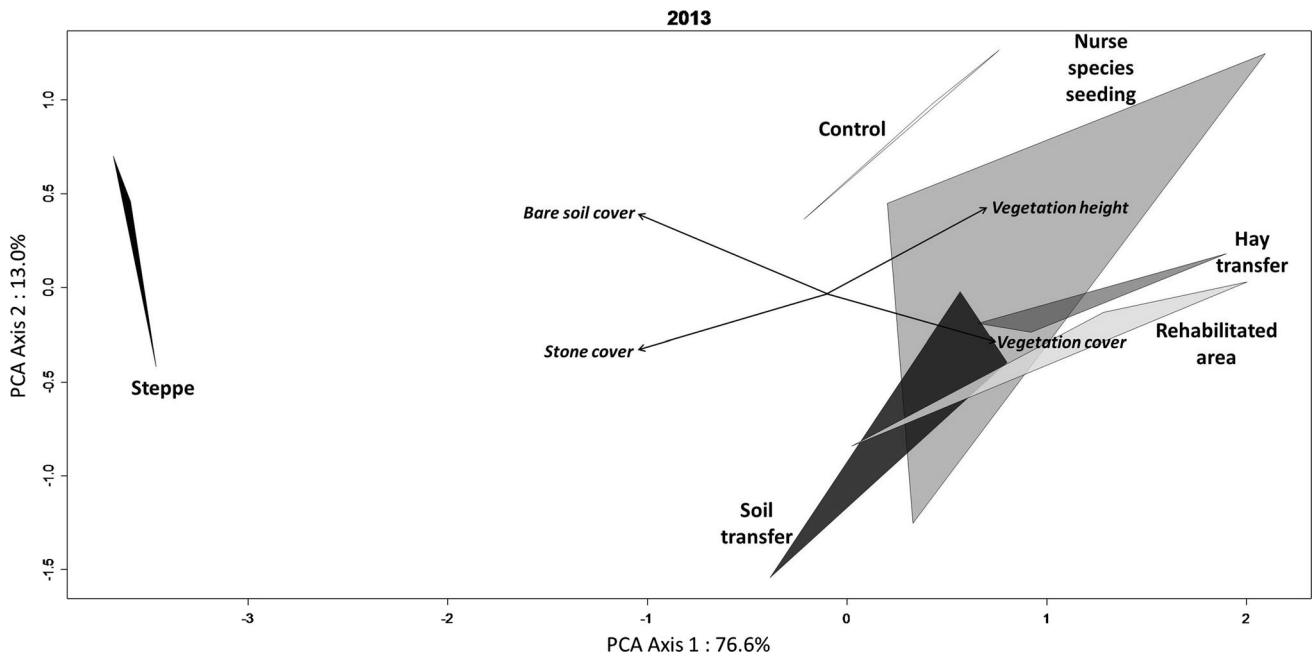


Fig. 4 PCA ordination based on habitat characteristics (bare soil cover; stone cover; vegetation height; vegetation cover) from each area in 2013: control (white), rehabilitated (light gray), nurse species

seeding (NSS) (gray), hay transfer (dark gray), soil transfer (very dark gray) and steppe (black)

were no significant differences between the steppe and the rehabilitated area or the control. Orthoptera abundance in these two areas increased from the second year to the fourth, as in the steppe. However, the four-year study also highlighted strong variations in Orthoptera abundance from 1 year to another in the steppe. These variations were not found in the three restoration treatments, which suggested that, rather than favoring Orthoptera abundance, they acted as buffers for Orthoptera dynamics. Measuring composition showed the Orthoptera species found in the restored and rehabilitated areas to be the typical species of the steppe. This contrasted with findings on vegetation (Jaunatre et al. 2014) and beetles (Alignan et al. 2013), other taxonomic groups considered in this rehabilitation and restoration project, which showed non-target species to have colonized the Cossure area. Our results suggest that Orthoptera have a more rapid response, as typical Orthoptera composition was reached over such a short period. Nevertheless, these results on composition should be taken as preliminary: the NMDS on the trajectories of the barycenter of all areas showed strong dynamics, which means that the response can vary from 1 year to another. Thus, further monitoring will be necessary to assess whether these dynamics ultimately approach the steppe dynamics. Calculating the CSInorm showed that the proportion of Orthoptera species abundance in the control, rehabilitated and soil transfer areas did not significantly differ from the proportion of Orthoptera species abundance

in the reference ecosystem. Once again, nurse species seeding and hay transfer were significantly different from the steppe. To our knowledge, no studies have to date considered the impact of nurse species seeding; however, the impact of hay has been studied and proved to be non-significant for grasshoppers (Kiehl and Wagner 2006) but also to successfully transfer grasshoppers (Wagner 2004). With the HAI, the non-significant differences between the steppe and all the other areas showed that target species abundance in the control, restored and rehabilitated areas did not increase significantly above their abundance in the reference ecosystem. Thus, based on these two indices, we can conclude that the structure of the Orthoptera assemblages in all areas except nurse species seeding and hay transfer was close to that found in the steppe.

One method often considered to favor colonization of Orthoptera is translocation or reinforcement. Experiments have been performed with varying degrees of success (Pearce-Kelly et al. 1998; Sherley 1998; Berggren 2005; Stringer 2005; Wagner et al. 2005; Hochkirch et al. 2007; Watts et al. 2008). In our study on Orthoptera, this does not appear a useful option. Given (1) the risk of failures such as those encountered in the course of previous studies (unsuitable habitat; unfavorable climatic period; insufficient number of individuals considered), (2) the absence of a context of urgency in our study area because no species threatened with extinction like *Prionotropis hystrix rhodanica* (Foucart and Lecoq 1998) or with a protection

status like or *Saga pedo* (Holuša et al. 2013) are present in the local area, and (3) since our results show rapid achievement of rehabilitation, we consider it unnecessary to attempt a translocation or reinforcement operation in future. Instead, monitoring will continue to measure whether abundance and structure are well achieved within the next few years.

Habitat quality

Habitat quality can affect Orthoptera, along with other factors like microclimate and soil characteristics. Our study shows that, 4 years after restoration and rehabilitation, the steppe habitat remains markedly different from the habitat in control, restored and rehabilitated areas. The tall and profuse vegetation cover that characterizes the control, restored and rehabilitated areas proves that the habitat is not yet the same as the original steppe. Vegetation height has already been proved to be significantly correlated (positively or negatively) with Orthoptera (Báldi and Kisbenedek 1997; Gardiner et al. 2002; Batáry et al. 2007; Picaud and Petit 2007). Vegetation cover is also important for Orthoptera (Clark 1948; Gardiner et al. 2002), and the patches of bare soil and stone cover characteristic of the steppe will need to increase in the next few years if the typical steppe habitat is to be recovered.

The importance of a multi-taxonomic approach in ecological restoration

In ecological restoration projects, at community scale, most studies deal with seed banks or with vegetation. Among fauna, birds are the main taxonomic group considered. In our project, one of the main goals was the return of typical steppe birds. During the first years after the abandonment of the orchard, steppe birds were encountered on the site (Wolff 2010). The study on vegetation showed that the rehabilitated area was colonized by vegetation differing from that of the steppe and that soil transfer was effective in achieving reasonable similarity in richness, diversity and composition with the steppe (Jaunatre et al. 2014). Our study on Orthoptera confirms the need to consider insects, as their response can differ from other taxonomic groups considered in ecological restoration. Combining the study of birds, vegetation and insects is therefore desirable. Here, if birds alone are considered, the restoration could be considered complete; but when insects are taken into account, it is clear that restoration has not accelerated natural recolonization by Orthoptera. While their presence confirms the emergence of a habitat favorable to entomofauna, their significantly low abundance is proof that the restored habitats (nurse species seeding, hay transfer, soil transfer) are not yet totally suitable. The differing

responses of avifauna, vegetation and insects point to the desirability of a multi-taxonomic approach, whenever possible, so as to obtain the most thorough evaluation of an ecological restoration project.

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